Journal of Urban Ecology

Journal of Urban Ecology, 2020, 1–11

doi: 10.1093/jue/juaa011
Research article

Differences in body composition between urban and rural Mallards, *Anas platyrhynchos*

Tyler E. Jarman,[1,*] Brett D. Gartrell[2] and Phil F. Battley [1]

[1]Wildlife and Ecology Group, School of Agriculture and Environment, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand; and [2]Wildbase, School of Veterinary Science, Massey University, Private Bag 11-222, Palmerston North 4442, New Zealand

*Corresponding author. E-mail: tyler.e.jarman@gmail.com

Submitted: 24 September 2019; **Received (in revised form):** 19 February 2020; **Accepted:** 19 March 2020

Abstract

Anthropogenic feeding of wildlife provides a valuable opportunity for people to engage with animals, but such feeding has the potential to be detrimental to the species involved. Ducks are frequently fed at urban ponds globally, yet the health impacts of an urban lifestyle for birds are poorly documented. We studied urban and rural Mallards (*Anas platyrhynchos*) in the Manawatū-Whanganui region (New Zealand). Mallards are opportunistic omnivores that have a phenotypically flexible gastrointestinal system. As urban Mallards consume considerable amounts of low-fibre, high carbohydrate foods via anthropogenic feeding, we predicted that urban Mallards would have smaller gastrointestinal tract organs and higher fat levels than rural ducks. We compared gross body composition of Mallards in a modified environment with high levels of feeding by humans and in rural habitats. We also evaluated other health-associated aspects including fat deposit size, liver fat content and haemosiderin (liver iron deposit) levels. Contrary to predictions, urban birds had larger gizzards and caeca and were no fatter than rural birds; rural birds additionally had larger pectoralis major muscles. These differences are probably associated with broader ecological and behavioural factors than with the provision of anthropogenic food per se [in particular the presence of hard foods (acorns and nuts) for urban birds, and higher flight activity of rural birds]. Longer caeca in urban birds could, however, relate to immunity rather than microbial fermentation of cellulose. Overall, while the nature of the local environment does affect Mallard physiology, no detrimental effects of urban living were evident in this study.

Key words: waterfowl, body composition, diet, urbanisation, anthropogenic feeding

Introduction

With an increasingly urban human population (Oro et al. 2013; McDonnell 2015), more people are becoming limited in their engagement with wildlife (Jones 2011a). One of the methods people in urban areas are engaging with nature is through their local parks by feeding animals natural and anthropogenic foods (Jones 2011b; Cox and Gaston 2018). In New Zealand, 46.6% of households engage in wildlife feeding, with bread constituting 88.1% of the food offered (Galbraith et al. 2014). Given that urban landscapes have been altered for human needs and as anthropogenic foods are absent in the wild, there is a difference in food availability between the urban and rural settings (Chace and Walsh 2006; Amrhein 2014). Changes in food availability and diet will likely affect the total quantity of fats, proteins and carbohydrates that urban wildlife will ingest (Kohl et al. 2017). Although anthropogenic foods can provide enough energy to meet metabolic needs, insufficient macronutrients in anthropogenic foods can have detrimental effects on the body condition of urban species (see Murray et al. 2018).

The digestive tracts of birds are known to be highly phenotypically flexible and responsive to the composition and nutritional value of the foods being digested (Battley and Piersma 2005; Champagnon et al. 2012). It has been suggested that having a gastrointestinal (GI) tract that responds to food availability

ensures optimal digestion of nutrients and reduces metabolic costs associated with an inefficient GI system (Battley and Piersma 2005; McWhorter et al. 2009). Organs that have been found to change in response to food quantity and intake are the gizzard, small intestine and liver (Battley and Piersma 2005).

Mallards, *Anas platyrhynchos*, are opportunistic omnivores that have a highly responsive GI system. Miller (1975) found that the Mallards' GI tract rapidly changes in response to highly indigestible foods being introduced to the diet. A diet high in indigestible fibre has been shown to result in a significant elongation of the caeca, small intestine and large intestine (Miller 1976). The gizzard is a large and heavy organ in birds responsible for the mechanical breakdown of food, and its size can reflect the quantity and quality of foods being consumed (Moore 1998b). There may also be pressures to minimise mass to help facilitate flight (Moore 1998a).

Given that the diet of a Mallard varies between habitats as food availability and abundance differs, i.e. fish, insects, molluscs, plant material, seeds (see Jorde et al. 1983; Khan et al. 1996; Guillemain et al. 2000; Arzel and Elmberg 2004; Chapman and Jones 2011), and their GI tract responds to the types of foods being ingested, it is likely that consumption of anthropogenic foods in urban areas results in changes in the GI tract. Specifically, if birds are eating lower fibre foods, we would predict shorter GI tracts and smaller gizzards in urban birds. Additionally, the greater intake of carbohydrates from anthropogenic food and lack of foraging effort required to obtain it raises the possibility that there are direct health impacts (i.e. increased fat levels) for Mallards with an urban lifestyle.

In this study, we compare the body composition of rural and urban Mallards in New Zealand. We compare the masses of dissected muscle and digestive organs, and fat deposits, between rural and urban birds. We also test for differences in fat accumulation (excessive caloric intake to energy expenditure ratio) and metal deposition (accumulation of iron from the diet) in the liver to assess for potential organ damage and disease between the two habitats. The combination of these should reveal whether there are discernible diet-related impacts on the internal morphology and health of urban ducks at a site regularly provisioned with anthropogenic foods.

Methods

Animal collection

Adult Mallards were collected over a 10-week period between February and May 2018. Urban ducks were collected from the Victoria Esplanade (40°22′15.1″S 175°37′03.0″E) and the Hokowhitu Lagoon (40°22′09.8″S 175°37′45.1″E) (Fig. 1) in Palmerston North, New Zealand, captured by hand or by walk-in cage trap. The population of Mallards at the Victoria Esplanade (the main urban study site) averages around 130 birds in summer and 100 birds in winter (Jarman 2019). Rural Mallards were captured using baited walk-in cage traps across multiple sites across the Manawatū-Whanganui region (40°18′15.9″S 175°30′22.6″E, 40°18′29.9″S 175°41′01.3″E, 40°18′06.9″S 175°45′53.6″E). Additional rural Mallards were donated by Fish and Game Wellington from reclaimed illegally shot game (40°18′15.9″S 175°30′22.6″E). Ducks captured live were euthanased by sedation with an intramuscular injection of 1.0 mg/kg of midazolam and 4.0 mg/kg of butorphanol followed by an intravenous injection of 150 mg/kg of pentobarbital. In total, we analyse 12 rural females and 8 rural males, and 11 urban females and 10 urban males.

Morphometric assessments

Prior to dissection, bill length, total head length and tarsus were measured (using Vernier callipers to ±0.1 mm). Wing length was recorded using the maximum chord method (Spencer 1976) by flattening the wing along a steel ruler (±1 mm), and body mass was recorded on a digital scale (±1 g). During dissection, the right-hand side of the keel and the right coracoid were exposed. Four measurements of the keel and coracoid were taken in accordance with Piersma et al. (1984, measurements a–d in their figure 1, representing keel length, width and depth and the length from the keel to the distal end of the coracoid). The right-hand side pectoralis major and supracoracoideus muscles were removed and collected, then the entire keel removed to expose the cardiovascular organs and GI tract. The right leg was also removed, and muscles dissected out.

Before removal, the heart width (greatest width from right atrium to left atrium), length (greatest length from right atrium to apex) and coronary band thickness (greatest width of fat) were measured (±0.1 mm). Each heart chamber was opened and rinsed with water to remove any congealed blood prior to drying. The liver was measured *in situ* along the body axis (length ±0.1 mm) and carefully removed. The abdominal viscera were then removed and laid straight, but not stretched, on a wet surface. The spleen and mesenteries were removed leaving only the GI to be separated into the proventriculus, gizzard, small intestine (gizzard to the anterior junction of the caeca), large intestine (anterior junction of the caeca to the rectum) and caeca (as outlined by Moore and Battley 2006). The proventriculus length, large intestine length, and gizzard external length, width and depth were all measured (±0.1 mm). The gizzard was cut in two along the medial plane, allowing for gizzard muscle and koilin thickness (membrane formed by sections of glands of the gizzard) to be measured (thickest measurement taken ±0.1 mm). Lengths of the small intestine and each caecum were measured using a steel ruler (±1 mm).

All muscle, fat and organ samples were placed into pre-weighed, labelled aluminium dishes and the fresh weight recorded (±0.001 g). After the fresh weight of the liver was taken, a 1 cm cube of the liver was removed for histology and weighed. All samples were then dried at 70°C for 7 days before being cooled in a desiccator and reweighed to obtain the dry mass. The entire dried liver was placed into an envelope made of filter paper and individually submerged in a sealed glass bottle of 100 ml petroleum ether. The petroleum ether from each bottle was removed and replenished every 4 days until the mass of the liver did not change for two consecutive days. Fat mass of the liver was obtained by subtracting the fat-free dry mass from the dry mass, and the resulting fat mass was expressed as a percent of the dry mass. The dry mass of the liver was corrected to include the sample removed for histology before statistical analysis.

We used external (lengths of the bill, total head and tarsus) and internal (all four sternum measurements) bone measurements in principal component analyses (PCA) to produce overall measures of body size. Wing length was not included in the external PCA as some individuals were undergoing wing moult. We used component 1 of the PCA as a size measure and compared how well these PCA-derived size measures correlated with organ masses. While the external PCA explained 63% of the size variation between individuals, it was much less correlated with organ sizes than the internal PCA (which explained 52% of the variation in measurements). Therefore, we used PC1 of the internal size PCA as the size measure in analyses.

Figure 1: Maps of the study sites in the North Island of New Zealand, showing the location of the rural (upper left) and urban (lower left) capture sites in yellow (Victoria Esplanade is the left-hand point in the lower map).

Individual factor loadings were keel length 0.546, keel to coracoid length 0.590, keel width −0.216, keel depth 0.408 and coracoid length 0.374.

Liver histology

Formalin-fixed samples of liver were prepared using standard histological techniques and tissue staining as described in Cork (2000) to assess the degree of haemosiderin (iron-storage complex) and by Wight and Siller (1975) to assess lipid deposition in hepatocytes. A minimum of 20 high powered fields of hepatocytes was evaluated for each bird. A subjective score of 0–3 was assigned based on the presence of haemosiderin and lipid deposition. Haemosiderin deposition in the liver were assigned scores dependent on the quantity of pigmentation of the cytoplasm of hepatocytes and Kupffer cells: 0—no pigment present or only very occasional granules in the cytoplasm of hepatocytes, 1—pigment present in the cytoplasm of some hepatocytes and occasional Kupffer cells, 2—pigment present in the cytoplasm of most hepatocytes and regularly in Kupffer cells and 3—heavy load of pigment present in the cytoplasm of all hepatocytes and swelling the cytoplasm of Kupffer cells.

Lipid deposition in the liver was also assessed following a similar scoring system based on the presence of fat vacuoles in hepatocytes and severity of distortion of the hepatocytes: 0—no fat vacuoles present in hepatocytes, 1—occasional fat vacuoles in the cytoplasm of hepatocytes with no distortion of the hepatocyte size, 2—fat vacuoles common in hepatocytes with some associated swelling of the hepatocytes and 3—fat vacuoles present in the cytoplasm of all hepatocytes with associated swelling and distortion of the hepatocytes.

One urban female's liver was too severely autolysed to interpret with any confidence and therefore was excluded from the analysis.

Statistical analyses

All statistical analyses were conducted using program R (version 3.5.1) (R Core Team, 2019) and to a significance level of $P < 0.05$. Fat, organ and muscle dry weights were tested for normality using a Shapiro–Wilk test. Measurements and weights that did not follow a normal distribution were transformed using the Tukey transformation procedure in the 'rcompanion' package; this successfully normalised all non-normal variables with the exception of visceral fat mass. We tested for effects of habitat and sex on body composition via linear models ('lm' function) with habitat (rural and urban) and sex (male and female) as factors and body size (PC1 based on internal skeletal measurements) as a continuous additional covariate to account for differences in organ mass that may scale with size. Starting with a global model including interactions, the 'step' function in R was used to progressively simplify the candidate model via comparison of Akaike information criterion (AIC) values until the 'best' (lowest AIC) model was found. We compared all models within two AIC units of the selected models where model simplification was supported. In most cases (17 of 26), there was no change in the identification of significant variables but in eight cases the less well-supported models failed to detect a main significant effect present in the main model. Of the 33

models tested, 11 were not significant or the models simplified to a null model with no variables. All factors in the significant final models are listed in Table 1, and full model outputs are provided in the Supplementary materials. Organ data are summarised in the text and tables as means ± standard deviation. Scores from the liver histology haemosiderin and lipid deposition were compared using chi-squaretests. Where results are visualised using box plots, graphs can be intrupted by boxes enclose the 25th–75th percentiles and the median, whiskers extend to the range, or to 1.5 times the interquartile range with circles showing outliers outside this range.

The use of Mallards in this study was approved by the Massey University Animal Ethics Committee (17/92). Permission was granted by the New Zealand Fish & Game Council to collect Mallards for this study. Additionally, the Palmerston North City Council approved the conduct of this study on the public-owned property of the Victoria Esplanade, Palmerston North, New Zealand.

Results

Muscle and cardiovascular

On average, males were heavier than females (means of 1098.8±36.6 g for rural females, 1121.0±116.8 g for urban females, 1233.2 ± 135.5 g for rural males and 1185.0 ± 94.7 g for urban males) but this difference largely reflected the larger body sizes of males (the only significant factor affecting mass was size; Table 1). Controlling for size, there were no differences in body mass between sexes or sites. The pectoralis major muscle varied not only with size ($P = 0.007$), but also with habitat ($P = 0.021$), with significantly heavier muscles in rural than urban ducks. Neither supracoracoideus nor leg muscles differed significantly between sites or sexes (Fig. 2, though supracoracoideus almost did with sex), but leg muscle mass increased with body size ($P = 0.017$). The dimensions (length and width) of the heart differed between the sexes (larger in males; Table 1 and Fig. 2) but there was no significant variation in the coronary fat band width.

Digestive organs

Body size related to organ size for a range of digestive organs (liver length, proventriculus length, gizzard mass and length, small intestine mass and length, large intestine mass and caeca mass and longer caecum length), but habitat (urban versus rural) also affected gizzard mass and size (larger in urban birds) and caeca lengths (longer in urban birds) (Table 1 and Fig. 3). Gizzards were also larger in males (width of gizzard and thickness of the gizzard muscle), as was the length of the shorter caecum. Variation in liver mass, pancreas mass, proventriculus mass and large intestine length were not explained by the factors tested. The spleen varied in complex ways with habitat, sex and size, due largely to urban males having light spleens (Table 1). There was also an interaction in liver length, which increased less with size in males than females.

Fat deposits

Variation in fat masses was poorly explained by the models, with only a lower level of abdominal fat in urban birds being detectable (Table 1), though the general pattern was for urban birds to have lower fat levels (Fig. 4). Urban birds on average had around half the fat content in their livers compared with rural birds (Fig. 4).

Liver histology

There were no significant differences in haemosiderin (χ^2, df = 3, $P = 0.398$) or lipid (χ^2, df = 3, $P = 0.412$) deposits in the liver of rural or urban ducks. A high proportion of Mallards (13/23 rural, 12/17 urban) had a lipid deposit score of 0, whereas haemosiderin deposits were fairly evenly spread across all scores for both urban and rural Mallards (Fig. 5).

Discussion

We documented several differences in body composition between urban and rural Mallards, principally that the main flight muscles were larger in rural birds, and the gizzard and caeca were larger in urban birds. We did not have an *a priori* prediction about flight muscle mass but had predicted that urban birds would have smaller digestive organs than rural birds would. This prediction was made on the assumption that urban birds foraged primarily upon anthropogenic foods.

An effect of body size was present in the masses of a range of exercise and nutritional organs (leg muscles and the pectoralis major flight muscle; liver, intestines, caeca) but not in any fat deposits. It is not surprising that muscle mass increased with body mass given that larger muscles are needed to support the locomotion of larger individuals (Lindstrom et al. 2000; Biewener 2011), and this was true for both flight and leg muscles. Interestingly, the pectoralis major was larger in rural Mallards than in urban Mallards despite no difference in overall body weight or size between the groups, even when sex was accounted for. Rural Mallards are likely to have larger home ranges and therefore greater flight requirements than do urban birds. In the USA, Varner et al. (2014) found that the median home range of rural Mottled Ducks (*A. fulvigula*) was more than 65 times larger than that of urban ducks. Therefore, rural ducks probably forage over larger areas and spend more time flying than do urban ducks (Møller 2009; Bengtsson et al. 2014), resulting in larger flight muscle masses.

The digestive organs of birds are notable for their phenotypic flexibility (Piersma and van Gils 2011) and respond to the kinds of foods available in an individual's environment. Dietary fibre is known to have profound effects on the function and length of avian GI tracts (Clench and Mathias 1995; Battley and Piersma 2005; Durant 2013). Foods high in dietary fibre have low rates of digestibility and the lengthening of the intestine allows for a greater quantity of food to be accommodated and therefore processed, increasing digestive efficiency (Moss 1989). Additionally, a large gizzard mass is required to provide the mechanical forces required to shear the bonds of structural fibre, thus many grazing species have large muscular gizzards (Moore 1998a). Given that the diet of urban ducks includes a substantial contribution of anthropogenic foods, we expected that urban Mallards would have shorter GI tracts than rural Mallards (as anthropogenic foods would not need hindgut fermentation to break down the complex bonds between molecules: Svihus et al. 2013) and smaller gizzards (due to lower levels of indigestible fibre in the urban diet).

Instead, we found the opposite: urban Mallards had larger gizzards in addition to having longer caeca compared with rural Mallards. This suggests that urban Mallards have a high intake of dietary fibre or additionally forage on other food items that require mechanical force to process (Miller 1975). The hardness of food has been also shown to increase the size of gizzards (Richardson and Wooller 1990), and experimental work with shellfish-crushing Red Knots (*Calidris canutus*) shows their

Table 1: Body composition variation in urban and rural Mallards. Subtext under table for explanation: Statistical results: coefficient ± standard errors for significant models with factors P<0.05 in bold, P<0.1 (trend) plain, and asterisks for non-significant factors retained in the model. Non-significant models shown as grey.

										Female		Male	
		F_{df}	P	R^2	Habitat	Sex	Size	Interactions		Rural	Urban	Rural	Urban
Total body	Mass	$18.65_{1,39}$	<0.001	0.31			1157.171 ± 15.876			1098.8 ± 96.6	1121.0 ± 116.8	1233.2 ± 135.5	1185.4 ± 94.7
Muscle masses	Pectoralis major (g)	$6.85_{2,38}$	0.003	0.23	**−2.5250 ± 1.0489**		**0.9156 ± 0.3238**			27.592 ± 2.382	25.450 ± 2.465	29.515 ± 4.988	26.699 ± 4.086
	Supracoracoideus (g)	$4.00_{1,39}$	0.052	0.07		0.09840 ± 0.04915				3.633 ± 0.384	3.827 ± 0.726	3.999 ± 0.375	3.628 ± 0.565
	Leg (g)	$6.32_{1,39}$	0.016	0.12			**0.004817 ± 0.001916**			9.746 ± 1.383	10.247 ± 1.835	11.291 ± 2.108	10.697 ± 1.791
Heart	Mass (g)	$2.41_{3,37}$	0.082	0.10						9.129 ± 0.702	8.721 ± 0.913	10.120 ± 1.988	9.934 ± 1.172
	Length (mm)	$4.30_{2,38}$	0.021	0.14	*	**2.4263 ± 0.9766**				39.7 ± 3.8	42.1 ± 3.8	42.9 ± 2.3	43.6 ± 1.7
	Width (mm)	$4.27_{3,37}$	0.011	0.20	*	**4.5114 ± 1.3316**	*	Habitat×sex	*	28.4 ± 4.4	30.0 ± 3.4	32.9 ± 1.8	31.7 ± 1.9
	Band thickness (mm)	$1.53_{3,37}$	0.222	0.04						6.0 ± 1.3	7.2 ± 2.2	6.7 ± 1.5	5.8 ± 1.0
Liver	Mass (g)	$1.90_{7,33}$	0.102	0.14						9.769 ± 3.689	9.564 ± 1.980	11.592 ± 3.039	10.855 ± 2.303
	Length (mm)	$4.26_{3,37}$	0.011	0.20		*	**0.0003040 ± 0.0001021**	Sex×size	**−0.0004375 ± 0.0001999**	79.9 ± 11.0	79.0 ± 6.3	81.8 ± 5.4	83.4 ± 3.9
Pancreas	Mass (g)	$1.78_{7,33}$	0.125	0.12						0.882 ± 0.260	0.859 ± 0.297	1.100 ± 0.251	1.097 ± 0.359
Spleen	Mass (g)	$2.24_{7,33}$	0.056	0.18	*	0.5681 ± 0.3356	*	Habitat×sex	*	0.116 ± 0.040	0.151 ± 0.072	0.190 ± 0.087	0.131 ± 0.055
								Habitat×size	**−0.3871 ± 0.1535**				
								Sex×size	*				
								Habitat ×sex×size	**0.6605 ± 0.3143**				
Proventriculus	Mass (g)	$1.65_{7,33}$	0.157	0.10						0.897 ± 0.250	1.133 ± 0.372	1.124 ± 0.382	0.886 ± 0.181
	Length (mm)	$6.01_{5,35}$	<0.001	0.39	*	*	**1.070e−04 ± 3.085e−05**	Habitat×sex	*	35.8 ± 3.3	36.7 ± 3.5	41.6 ± 4.9	37.5 ± 3.7
Gizzard	Mass (g)	$8.52_{2,38}$	<0.001	0.27	**−0.066383 ± 0.002376**		**0.002406 ± 0.001107**			9.550 ± 1.453	11.146 ± 2.075	9.981 ± 0.989	12.978 ± 2.950
	Length (mm)	$7.77_{2,38}$	0.002	0.25	**3.6352 ± 1.1090**		**0.7433 ± 0.3424**			39.0 ± 3.2	42.5 ± 4.2	41.1 ± 3.4	45.1 ± 3.5
	Width (mm)	$7.92_{3,37}$	<0.001	0.34	**4.5836 ± 1.1895**	**3.4361 ± 1.1838**				51.1 ± 3.0	56.0 ± 4.8	54.8 ± 2.8	59.0 ± 4.7
	Depth (mm)	$6.34_{2,38}$	0.004	0.21	**2.5240 ± 0.8071**	1.4513 ± 0.8033				30.6 ± 2.6	32.4 ± 2.8	31.4 ± 1.6	34.7 ± 3.2
	Muscle thickness (mm)	$19.77_{2,38}$	<0.001	0.48	**0.025426 ± 0.004409**	**−0.010145 ± 0.004388**				18.6 ± 3.3	23.5 ± 3.4	16.3 ± 2.1	21.8 ± 2.9
	Koilin thickness (mm)	NA	NA	NA						2.7 ± 0.5	2.6 ± 0.4	2.4 ± 0.5	2.6 ± 0.4
Small intestine	Mass (g)	$7.00_{1,39}$	0.012	0.13			**0.2867 ± 0.1084**			5.721 ± 1.253	5.365 ± 1.206	6.6334 ± 1.323	5.860 ± 0.781
	Length (mm)	$9.6_{2,38}$	<0.001	0.30	56.386 ± 31.518		**38.875 ± 9.731**			1399.6 ± 88.3	1474.7 ± 127.1	1512.4 ± 136.8	1555.6 ± 54.8
Large intestine	Mass (g)	$3.13_{7,33}$	0.011	0.27	*	*	**0.4420 ± 0.1425**	Habitat×sex	*	0.538 ± 0.184	0.670 ± 0.259	0.514 ± 0.101	0.615 ± 0.208
								Habitat×size	*				
								Sex×size	*				
								Habitat ×sex×size	0.7696 ± 0.4258				
	Length (mm)	$1.51_{7,33}$	0.200	0.08						86.1 ± 5.6	91.0 ± 12.1	88.7 ± 7.8	95.3 ± 18.3
Caeca	Mass (g)	$3.61_{7,33}$	0.005	0.31	*	*	**0.11025 ± 0.03087**	Habitat×sex	*	0.561 ± 0.124	0.610 ± 0.067	0.616 ± 0.128	0.727 ± 0.208
								Habitat×size	0.08442 ± 0.13422				
								Sex×size	−0.10036 ± 0.05720				
								Habitat ×sex×size	0.17029 ± 0.09225				
	Shorter length (mm)	$8.21_{2,38}$	0.001	0.27	**14.714 ± 5.402**	**16.612 ± 5.376**				126.5 ± 20.9	143.2 ± 14.2	145.0 ± 20.5	157.4 ± 7.0
	Longer length (mm)	$12.96_{2,38}$	<0.001	0.37	**22.583 ± 5.356**		**3.776 ± 1.381**			136.0 ± 22.9	162.3 ± 14.2	152.3 ± 15.4	172.4 ± 13.4
Fat masses	Furcular (g)	NA	NA	NA						2.124 ± 1.177	2.361 ± 1.982	2.027 ± 1.818	1.410 ± 0.792
	Abdominal (g)	$3.72_{1,39}$	0.06	0.06	−0.6378 ± 0.3307					4.590 ± 3.132	3.027 ± 2.564	6.186 ± 5.075	2.002 ± 1.314
	Visceral (g)	$1.74_{3,37}$	0.18	0.05						1.700 ± 1.370	1.895 ± 2.083	2.796 ± 2.872	0.383 ± 0.387
	Leg (g)	NA	NA	NA						1.566 ± 0.981	1.835 ± 1.382	1.707 ± 1.238	1.244 ± 0.743
	Total (g)	$1.68_{3,37}$	0.19	0.05						9.979 ± 5.783	9.117 ± 7.463	12.716 ± 10.499	5.038 ± 2.942
Liver fat mass	Percentage (%)	$3.91_{4,36}$	0.01	0.23	**−0.32267 ± 0.11846**	*	*	Sex×size	0.20465 ± 0.11569	6.38 ± 4.27	3.35 ± 2.42	7.01 ± 3.49	3.82 ± 1.84

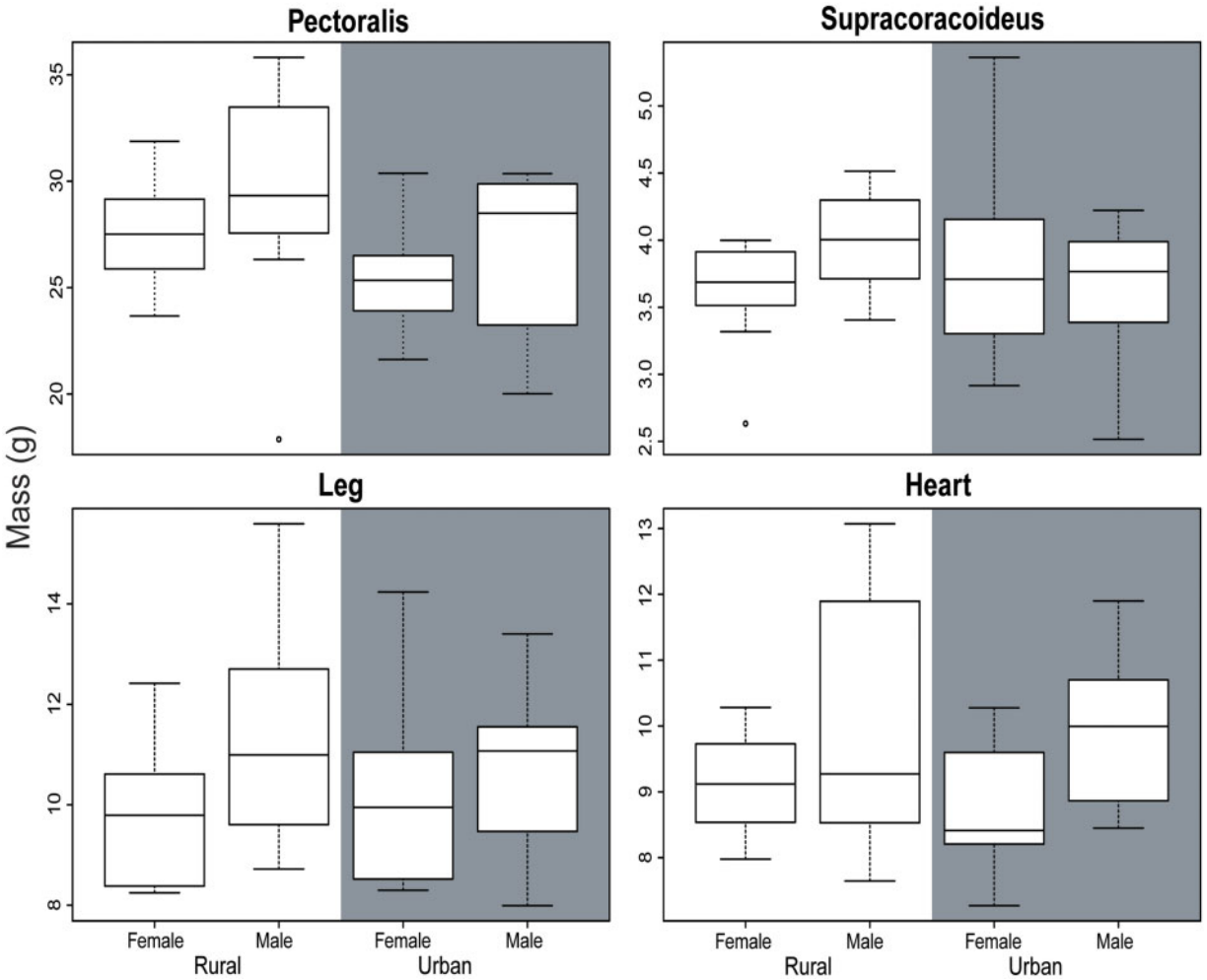

Figure 2: Dried mass of skeletal and cardiovascular muscles of rural and urban Mallards (Sample sizes from left to right = 12, 8, 11 and 10).

gizzards can increase in size by almost 150% in 6 days when hard food items are introduced to the diet (Dekinga et al. 2001). The local environment at the Victoria Esplanade includes numerous oak trees and palm trees, and Mallards have been observed foraging on both acorns and palm seeds (T.E.J. and P.F.B., pers. obs.)—this is likely the cause of their enlarged gizzards. Mechanical pressure produced increases in proportion to gizzard muscle thickness (Moore 1998a), and a larger gizzard allows greater processing rates of hard material (van Gils et al. 2003). Additionally, as urban Mallards are probably flying less than their rural conspecifics (Varner et al. 2014), they may not need to reduce their gizzard size, and hence total body weight, to facilitate flight (Moore 1998a).

High food intakes in urban Mallards, from either anthropogenic or natural sources, would result in lengthening of the GI tract (Miller 1975, 1976; Karasov 1996). In our study, however, the size of the GI tract typically increased with body size and not between urban and rural environments. This makes sense as a larger GI tract is required to meet the metabolic demands of a larger body (Miller and Eadie 2006). In saying that, there will be an increase in basal metabolic cost to maintain a larger GI tract (Battley and Piersma 2005), which in turn would reduce the excess energy available to convert into fat. Although many digestive organs in our study increased in size in proportion to body size, two digestive organs did differ in size between rural and urban environments, the gizzard and caeca.

The caeca have multiple functions in birds including microbial fermentation, water and nitrogen absorption and immunosurveillance (Klasing 1998). High intakes of dietary fibre in the diets of Mallards can also affect caeca length (Miller 1975, 1976; Kehoe et al. 1988; Clench and Mathias 1995). We found that urban Mallards had larger caeca that rural Mallards. It is unlikely that urban birds had a high-fibre diet (Ottoni et al. 2009), and an alternative explanation for their longer caeca is that they could play a greater role in immunosurveillance in the high-density urban environment where the risk of disease is greater (Clench and Mathias 1995; Murray et al. 2016). Additionally, urban Mallards have been found to have higher levels of microfungal biotic diversity than rural Mallards (Meissner et al. 2015). Therefore, the elongation of caeca could be the result of the continuous immune response to individuals living in a habitat where contact with different pathogens is common (Clench and Mathias 1995). Parasite infestation is also known to influence fat deposits of individuals, as the uptake of nutrients and energy from food ingested will divert to the

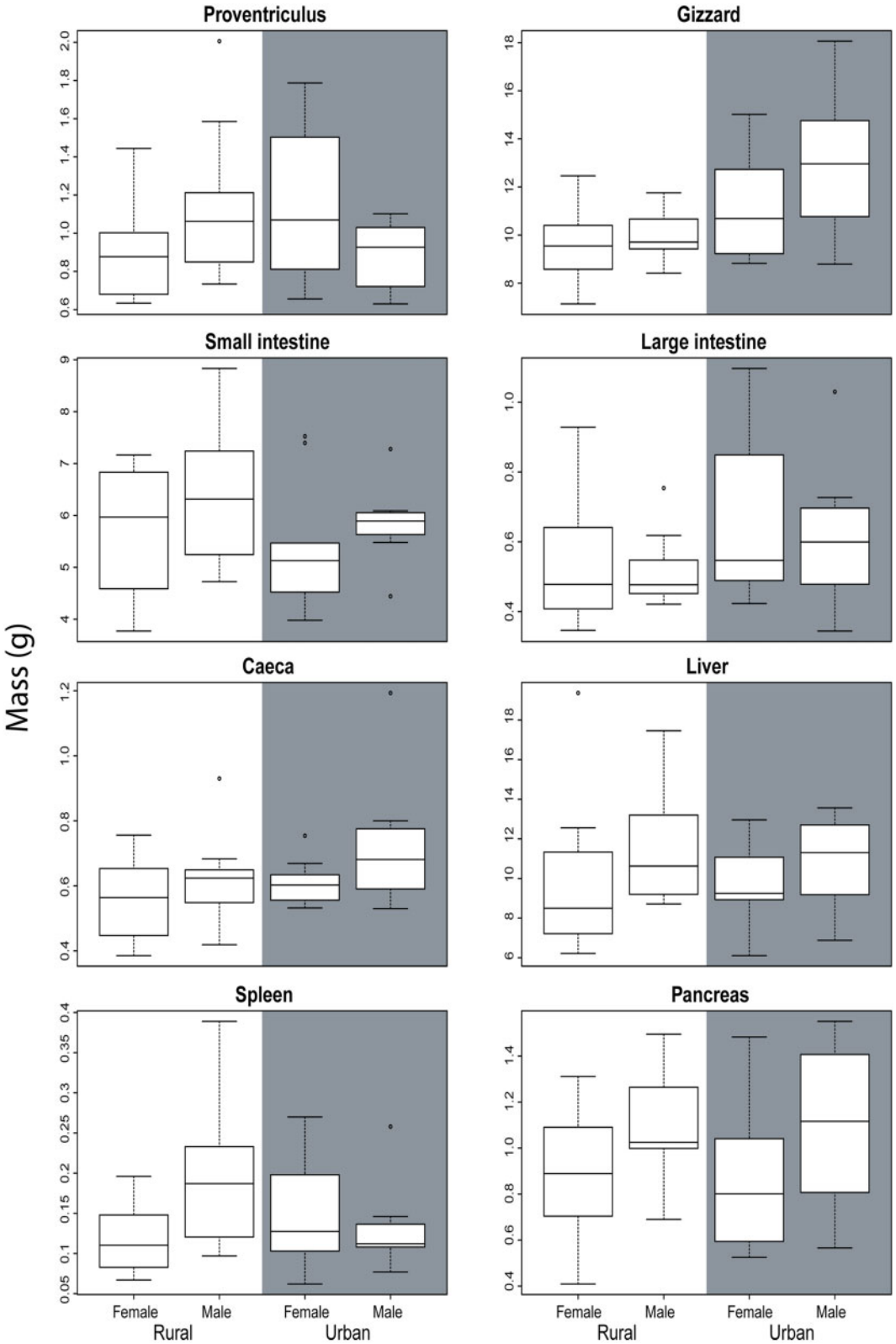

Figure 3: Dried organ masses in urban and rural Mallards (Sample sizes and box conventions as in Fig. 2.).

parasite from the host (Brown et al. 1995), reducing the total energy available to the host species.

As anthropogenic foods such as bread are typically high in carbohydrates (Friedman 1996), and thus energy, it would be expected that urban Mallards would have large fat deposits due to excessive energy being converted to fat. However, there were no significant differences in fat deposits between the two groups. Urban birds having poorer body condition than their

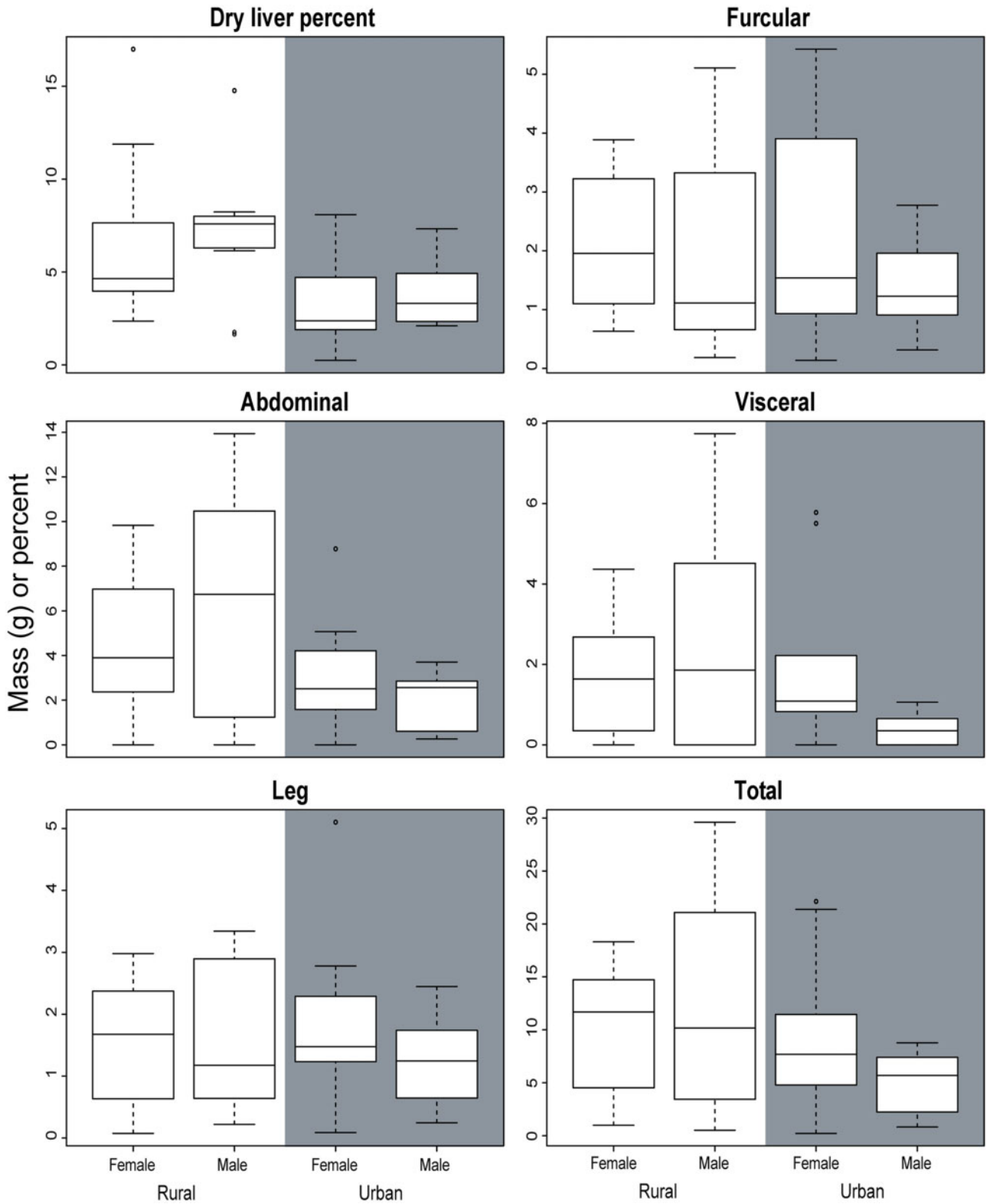

Figure 4: Dried fat masses in urban and rural Mallards; fat in the liver represents chemically extracted fat as a percent of the liver dry mass (Sample sizes as in Fig. 2.).

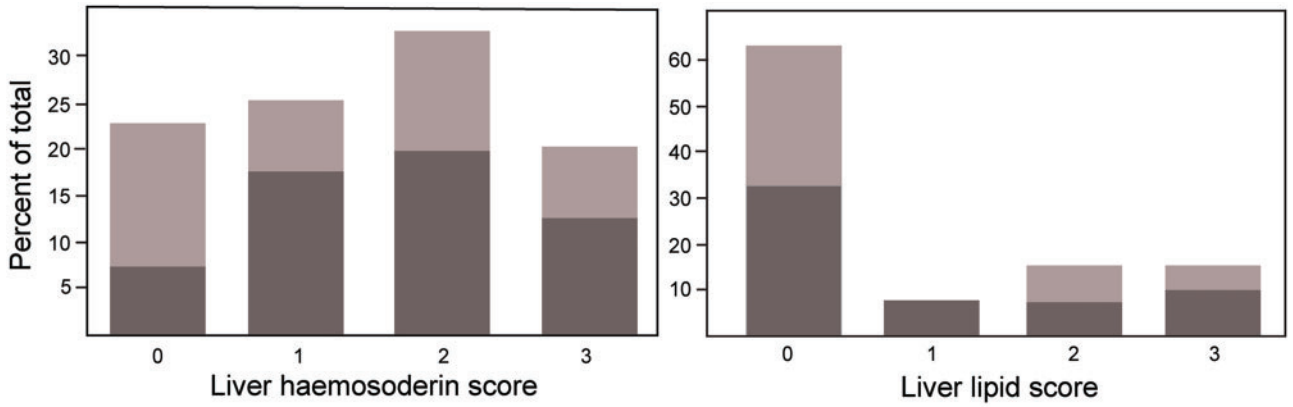

Figure 5: Haemosiderin (left) and lipid (right) deposition in the liver were assigned scores dependent on the severity of their presence in the hepatocytes (Dark grey = urban, n 17; light grey = rural, n 23).

rural conspecifics has also been seen in the American white ibis (*Eudocimus albus*) (Murray et al. 2018) and House Sparrow (*Passer domesticus*) (Liker et al. 2008).

This could be a result of the predictable nature of the anthropogenic food supply meaning that birds do not need substantial fat stores as an energy buffer. Males tended to dominate food hand-outs (T.E.J., pers. obs.), and the lower fat levels in urban males could mean that they, in particular, need less of an energetic buffer than females do. An alternative explanation could be the 'credit card' hypothesis (Shochat 2004). In this, the predictable food supply and low predation risk at urban sites allow excessively high populations to congregate, despite them exceeding the local carrying capacity. This results in many birds being in poor condition, with just a few 'winners' expected to dominate the food resources, and urban birds would have poorer body condition than individuals in a more natural environment (Liker et al. 2008). It is suggestive that the leanest birds in our sample were urban males, implying that they might face the largest nutritional deficit.

Although urban species have lower predation risk and associated stresses, the urban environment can be just as stressful on urban species as rural environments are on their rural counterparts (Ditchkoff et al. 2006). Stress is known to cause weight loss in the long run as glycogen stored in the liver is broken down into glucose, thus drawing from the individual's energy reserves (Siegel 1980). Urban Mallards in our study had lower proportions of fat in their liver than rural Mallards. Additionally, when Mallards were captured for this study, both groups had just undergone the physiological process of moulting their flight feathers (Sheppard 2017). Moulting is physiologically expensive with Mallards having an estimated 30% increase in their basal metabolism to meet the energy required to undergo a complete moult (Fox et al. 2013). Mallards meet this increase in metabolic cost by drawing from their fat stores (Pehrsson 1987). This may explain why we found no difference in most discrete body fat positions in urban and rural birds. It is less clear why we found a difference in extracted liver fat levels between the two groups but no difference in histological lipid scores for the liver, with most birds having a score of zero (Fig. 5).

Although urban Mallards have been found to have greater iron concentrations in their blood than rural Mallards (Binkowski and Meissner 2013), we found no significant differences in haemosiderin between individuals from either habitat. This could be due to our urban site not having a history of industrial activity, or to rural mallards residing in or near intensified agricultural land, a known contributor to metals in soils and water (Mance 2012). Therefore, we cannot conclude if either population is experiencing greater levels of oxidative stress than the other (Koivula and Eeva 2010).

While this study was not an explicit test of the impact of feeding *per se*, the results showed that Mallards living an urban lifestyle—in which anthropogenic feeding plays a large role—results in differences in body composition. Whether all the differences we documented are related to diet and activity, or whether some represent responses to other challenges, is unclear. The longer caeca of urban birds may not be needed for hindgut fermentation to break down low-fibre anthropogenic food, so could potentially reflect immune challenges. Likewise, whether the lower fat levels in urban birds represent an inability to deposit fat, compared with it reflecting a lack of need of an energetic buffer, need further work.

The study site is in many ways a typical local council artificial pond, being easy to access for people, with a café and playground nearby, and is popular with young families who enjoy feeding the ducks. But it is also set near a remnant patch of native forest, has extensive exotic tree plantings and is close to a river. Mallards can be observed departing the pond at dusk and arriving after dawn, evidently having been feeding elsewhere, and a Global Positioning System (GPS)-tracked duck from the pond did visit the nearby Manawatu River (Jarman 2019). Despite having a regular supply of anthropogenic food, ducks using the site may still maintain a substantial level of natural foraging on the urban–rural fringe, and so these 'urban' ducks may be far less urban than birds in other locations and this may contribute to directions of the differences we found. Comparison of our results with birds from truly 'urban-locked' sites might clarify how site-specific any effects of urbanisation are.

Supplementary data

Supplementary data are available at *JUECOL* online.

Acknowledgements

We are grateful to all the private landowners who allowed us to work on their lands, and to the Palmerston North City Council for allowing us to work on government-owned land.

We wish to express our gratitude towards Fish and Game Wellington for their assistance in collection of Mallards used in this study.

Funding

This research received financial support from the Wildbase Research Trust Research Fund, Massey University, New Zealand.

Data availability

Data sets used for analyses in this study are available upon request to the corresponding author.

Conflict of interest statement. None declared.

References

Amrhein, V. (2014) 'Wild Bird Feeding (Probably) Affects Avian Urban Ecology', in G. Diego and B. Henrik (eds) *Avian Urban Ecology: Behavioural and Physiological Adaptations*, pp. 29–38. Oxford: OUP.

Arzel, C. and Elmberg, J. (2004) 'Time Use, Foraging Behavior and Microhabitat Use in a Temporary Guild of Spring-Staging Dabbling Ducks (*Anas* spp.)', *Ornis Fennica*, **81**: 157–68.

Battley, P. F. and Piersma, T. (2005) 'Adaptive Interplay Between Feeding Ecology and Features of the Digestive Tract in Birds', in J. M. Starck and T. Wang (eds) *Physiological and Ecological Adaptations to Feeding in Vertebrates*, Vol. **81**, pp. 201–228. Enfield, New Hampshire: Science Publishers.

Bengtsson, D. et al. (2014) 'Movements, Home-Range Size and Habitat Selection of Mallards During Autumn Migration', *PLoS One*, **9**: e100764–14.

Biewener, A. A. (2011) 'Muscle Function in Avian Flight: Achieving Power and Control', *Philosophical Transactions of the Royal Society B: Biological Sciences*, **366**: 1496–506.

Binkowski, L. J. and Meissner, W. (2013) 'Levels of Metals in Blood Samples from Mallards (*Anas platyrhynchos*) from Urban Areas in Poland', *Environmental Pollution*, **178**: 336–42.

Brown, C. R., Brown, M. B., and Rannala, B. (1995) 'Ectoparasites Reduce Long-Term Survival of Their Avian Host', *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **262**: 313–19.

Chace, J. F., and Walsh, J. J. (2006) 'Urban Effects on Native Avifauna: A Review', *Landscape and Urban Planning*, **74**: 46–69.

Champagnon, J. et al. (2012) 'Low Survival After Release into the Wild: Assessing "the Burden of Captivity" on Mallard Physiology and Behaviour', *European Journal of Wildlife Research*, **58**: 255–67.

Chapman, R. and Jones, D. N. (2011) 'Foraging by Native and Domestic Ducks in Urban Lakes: Behavioural Implications of All That Bread', *Corella*, **35**: 101–6.

Clench, M. H. and Mathias, J. R. (1995) 'The Avian Cecum: A Review', *The Wilson Bulletin*, **107**: 93–121.

Cork, S. C. (2000) 'Iron Storage Diseases in Birds', *Avian Pathology*, **29**: 7–12.

Cox, D. T. and Gaston, K. J. (2018) 'Human–Nature Interactions and the Consequences and Drivers of Provisioning Wildlife', *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**: 20170092–9.

Dekinga, A. et al. (2001) 'Time Course and Reversibility of Changes in the Gizzards of Red Knots Alternately Eating Hard and Soft Food', *Journal of Experimental Biology*, **204**: 2167–73.

Ditchkoff, S. S., Saalfeld, S. T., and Gibson, C. J. (2006) 'Animal Behavior in Urban Ecosystems: Modifications Due to Human-Induced Stress', *Urban Ecosystems*, **9**: 5–12.

Durant, D. (2013) 'The Digestion of Fibre in Herbivorous Anatidae: A Review', *Wildfowl*, **54**: 7–24.

Fox, A. D., King, R., and Owen, M. (2013) 'Wing Moult and Mass Change in Free-Living Mallard *Anas platyrhynchos*', *Journal of Avian Biology*, **44**: 1–8.

Friedman, M. (1996) 'Nutritional Value of Proteins from Different Food Sources', *Journal of Agricultural and Food Chemistry*, **44**: 6–29.

Galbraith, J. A. et al. (2014) 'Risks and Drivers of Wild Bird Feeding in Urban Areas of New Zealand', *Biological Conservation*, **180**: 64–74.

Guillemain, M., Fritz, H., and Blais, S. (2000) 'Foraging Methods Can Affect Patch Choice: An Experimental Study in Mallard (*Anas platyrhynchos*)', *Behavioural Processes*, **50**: 123–9.

Jarman, T. E. (2019) 'Effects of Urbanization on the Feeding Ecology and Physiology of Mallards (*Anas platyrhynchos*)', MSc thesis, Massey University, New Zealand.

Jones, D. (2011a) 'An Appetite for Connection: Why We Need to Understand the Effect and Value of Feeding Wild Birds', *Emu: Austral Ornithology*, **111**: i–vii.

—— (2011b) 'Seeking Nature in the City: The Implications of Feeding Wildlife', *Paper presented at the ANZCCART*, Auckland, New Zealand.

Jorde, D. G., Krapu, G. L., and Crawford, R. D. (1983) 'Feeding Ecology of Mallards Wintering in Nebraska', *The Journal of Wildlife Management*, **47**: 1044–53.

Karasov, W. H. (1996) 'Digestive Plasticity in Avian Energetics and Feeding Ecology', in C. Carey (ed.) *Avian Energetics and Nutritional Ecology*, pp. 61–84. New York, NY: Chapman and Hall.

Kehoe, F. P., Ankney, C. D., and Alisauskas, R. T. (1988) 'Effects of Dietary Fiber and Diet Diversity on Digestive Organs of Captive Mallards (*Anas platyrhynchos*)', *Canadian Journal of Zoology*, **66**: 1597–602.

Khan, A. A. et al. (1996) 'Activity Budget Analysis of Non-Breeding Mallards (*Anas platyrhynchos*) at Sarp Lake, Turkey', *Pakistan Journal of Zoology*, **28**: 57–61.

Klasing, K. C. (1998) *Comparative Avian Nutrition*. Eastbourne, UK: Cab International.

Kohl, K. D. et al. (2017) 'Modulation of Digestive Enzyme Activities in the Avian Digestive Tract in Relation to Diet Composition and Quality', *Journal of Comparative Physiology B*, **187**: 339–51.

Koivula, M. J. and Eeva, T. (2010) 'Metal-Related Oxidative Stress in Birds', *Environmental Pollution*, **158**: 2359–70.

Liker, A. et al. (2008) 'Lean Birds in the City: Body Size and Condition of House Sparrows Along the Urbanization Gradient', *Journal of Animal Ecology*, **77**: 789–95.

Lindstrom, A. et al. (2000) 'Avian Pectoral Muscle Size Rapidly Tracks Body Mass Changes during Flight, Fasting and Fuelling', *Journal of Experimental Biology*, **203**: 913–9.

Mance, G. (2012) *Pollution Threat of Heavy Metals in Aquatic Environments*. Essex, England: Springer Science and Business Media.

McDonnell, M. J. (2015) 'Journal of Urban Ecology: Linking and Promoting Research and Practice in the Evolving Discipline of Urban Ecology', *Journal of Urban Ecology*, **1**: juv003–6.

McWhorter, T. J., Caviedes-Vidal, E., and Karasov, W. H. (2009) 'The Integration of Digestion and Osmoregulation in the Avian Gut', *Biological Reviews*, **84**: 533–65.

Meissner, W. et al. (2015) 'Mallards (*Anas platyrhynchos*) Staying in Urban Environments Have Higher Levels of Microfungi Biota Diversity Than Do Birds from Non-urban Areas', *Fungal Ecology*, **17**: 164–9.

Miller, M. R. (1975) 'Gut Morphology of Mallards in Relation to Diet Quality', *The Journal of Wildlife Management*, **39**: 168–73.

—— (1976) 'Cecal Fermentation in Mallards in Relation to Diet', *The Condor*, **78**: 107–11.

—— and Eadie, J. M. (2006) 'The Allometric Relationship Between Resting Metabolic Rate and Body Mass in Wild Waterfowl (Anatidae) and an Application to Estimation of Winter Habitat Requirements', *The Condor*, **108**: 166–77.

Møller, A. P. (2009) 'Successful City Dwellers: A Comparative Study of the Ecological Characteristics of Urban Birds in the Western Palearctic', *Oecologia*, **159**: 849–58.

Moore, S. J. (1998a) 'The Comparative Functional Gizzard Morphology of Several Species of Birds', *Australian Journal of Zoology*, **46**: 359–68.

—— (1998b) 'The Gizzard Morphology of an Avian Herbivore: The Domestic Goose, *Anser anser*', *Australian Journal of Zoology*, **46**: 345–57.

—— and Battley, P. F. (2006) 'Differences in the Digestive Organ Morphology of Captive and Wild Brown Teal *Anas chlorotis* and Implications for Releases', *Bird Conservation International*, **16**: 253–64.

Moss, R. (1989) 'Gut Size and the Digestion of Fibrous Diets by Tetraonid Birds', *Journal of Experimental Zoology*, **252**: 61–5.

Murray, M. H. et al. (2016) 'Wildlife Health and Supplemental Feeding: A Review and Management Recommendations', *Biological Conservation*, **204**: 163–74.

—— et al. (2018) 'From Wetland Specialist to Hand-Fed Generalist: Shifts in Diet and Condition with Provisioning for a Recently Urbanized Wading Bird', *Philosophical Transactions of the Royal Society B: Biological Sciences*, **373**: 20170100–10.

Oro, D. et al. (2013) 'Ecological and Evolutionary Implications of Food Subsidies from Humans', *Ecology Letters*, **16**: 1501–14.

Ottoni, I., de Oliveira, F. F. R., and Young, R. J. (2009) 'Estimating the Diet of Urban Birds: The Problems of Anthropogenic Food and Food Digestibility', *Applied Animal Behaviour Science*, **117**: 42–6.

Pehrsson, O. (1987) 'Effects of Body Condition on Molting in Mallards', *The Condor*, **89**: 329–39.

Piersma, T., Davidson, N., and Evans, P. (1984) 'Estimation of the Protein Reserves of Waders: The Use and Misuse of Standard Muscle Volume', *Wader Study Group Bulletin*, **42**: 19–22.

—— and van Gils, J. A. (2011). *The Flexible Phenotype: A Body-Centred Integration of Ecology, Physiology, and Behaviour*. Oxford: Oxford University Press.

R Core Team. (2018) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria, <https://www.R-project.org/> accessed 17 Apr 2020.

Richardson, K. C. and Wooller, R. D. (1990) 'Adaptations of the Alimentary Tracts of Some Australian Lorikeets to a Diet of Pollen and Nectar', *Australian Journal of Zoology*, **38**: 581–6.

Sheppard, J. (2017) 'Breeding Ecology and Productivity of Mallards and Mallard-Grey Duck Hybrids in New Zealand', PhD thesis, University of Auckland, New Zealand.

Shochat, E. (2004) 'Credit or Debit? Resource Input Changes Population Dynamics of City-Slicker Birds', *Oikos*, **106**: 622–6.

Siegel, H. (1980) 'Physiological Stress in Birds', *BioScience*, **30**: 529–34.

Spencer, R. (1976). *The Ringer's Manual*. Tring, Hertfordshire: British Trust for Ornithology.

Svihus, B., Choct, M., and Classen, H. (2013) 'Function and Nutritional Roles of the Avian Caeca: A Review', *World's Poultry Science Journal* , **69**: 249–64.

van Gils, J. A. et al. (2003) 'Cost-Benefit Analysis of Mollusc-Eating in a Shorebird. II. Optimising Gizzard Size in the Face of Seasonal Demands', *Journal of Experimental Biology*, **206**: 3369–80.

Varner, D. M., Hepp, G. R., and Bielefeld, R. R. (2014) 'Movements and Seasonal Use of Habitats by Rural and Urban Female Mottled Ducks in Southeast Florida', *The Journal of Wildlife Management*, **78**: 840–7.

Wight, P. and Siller, W. (1975) 'The Histopathology of Fatty Liver and Kidney Syndrome in Chicks', *Research in Veterinary Science*, **19**: 173–84.

Differences in body composition between urban and rural Mallards, Anas platyrhynchos

Jarman, TE

2020-01-01